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Confirmed presence of *Clathrus columnatus* Bosc (Phallales, Clathraceae) in the Galapagos Islands, Ecuador

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Abstract. In July 2022, we collected three groups of *Clathrus columnatus* Bosc (Clathraceae) specimens (four mature and eight immature basidiomata) from Santa Cruz Island, Galapagos. We report these specimens as the first confirmed records of this species from the Galapagos Archipelago and Ecuador. We hypothesize that *C. columnatus* constitutes a recent introduction to the islands. We provide macro- and microscopic descriptions, including photographs of fresh and fluid-preserved basidiomata, and comments on the species' taxonomy, ecology, and distribution.

Keywords. Basidiomycota, citizen science, clathroids, gasteroid fungi, introduced species, new record

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Introduction

Clathroids are a diverse group of fungi in the order Phallales and are characterized by their cage-shaped receptacle, mucilaginous gleba, and fetid odor, which are adaptations for spore dispersal by insects (Zeller 1949; Dring 1980). These Gasteromycetes are part of the Phallaceae *sensu lato* (Index Fungorum 2023), a family that has traditionally included stinkhorns and cage fungi. Recent molecular evidence shows the monophyly of the family Clathraceae, which includes the genera *Abrachium* Baseia & T.S. Cabral, *Aseroë* Labill., *Blumenavia* Möller, *Clathrus* P. Micheli ex L., *Ileodictyon* Tul. & C. Tul., *Laternea* Turpin, and *Pseudocolus* Lloyd (Melanda et al. 2021). Cabral et al. (2012) emended the description of Clathraceae, recognizing its members by their sessile or short-stalked basidiomata, which expand from a volva; with a spreading receptacle (sometimes arched and united columns or latticed), or an armless sunflower-shaped receptacle.

Clathrus species have several morphologies (Ribeiro et al. 2022), but they are mostly characterized by the position of the gleba which is inside the column-latticed basidiomata, not confined to a single glebifer (Dring 1980; Fazolino et al. 2010). The genus has a cosmopolitan distribution (Kotlaba and Zehnálek 2018). On mainland Ecuador, five *Clathrus* species are suspected but not confirmed. One specimen was reported by Læssøe and Petersen (2008) as *Clathrus* cf. *crispus*, and four observational records are included on the citizen-science platform iNaturalist: *C.* cf. *archeri*, *C.* cf. *cristatus*, *C.* cf. *natalensis*, and *C.* cf. *columnatus* (iNaturalistEc 2023). Few herbaria specimens are preserved in Ecuadorian repositories at the National Herbarium (QCNE) and at the Mycological collection of the Catholic University (QCAM). Identification of specimens at these institutions is ongoing (Batallas-Molina pers. comm. 2022; Caicedo pers. comm. 2022).

Mycological research in the Galapagos has a relatively short history. Reid et al. (1980) provided the largest

list of fungi from the archipelago, based principally on collections made by Evans and Cronshaw from Santa Cruz Island in 1976. In general, macrofungi collections have been scarce. During 2005–2008, a baseline fungal inventory was carried out on Santa Cruz Island (Bungartz et al. 2008). Most newly reported species belonged to Agaricales (Arturo 2008). An updated checklist of Basidiomycota was more recently published by Bates et al. (2014), in which the only Phallales species included was *Phallus indusiatus* Vent.; it was considered native to the archipelago. There are insufficient data about the origin of most species of fungi in the Galapagos. The islands are of volcanic origin and located in the Pacific Ocean roughly 1000 km off the coast of Ecuador. It is plausible that most species of fungi have historically reached the islands by natural means, such as on migratory birds (Ryvarden 2013). Nevertheless, it cannot be ruled out that several species have been introduced much more recently. As a result of human colonization, the number of alien, non-native species in the archipelago has risen considerably (Toral-Granda et al. 2017). Thus, it can be assumed that an unknown but large number of non-native fungi are now well established in the archipelago.

Here we document the presence of *Clathrus columnatus* Bosc in the Galapagos Islands, and our records of this species constitute the first confirmed from Ecuador. Our report is based on recent collections and observations in the agricultural areas of Santa Cruz Island. Although *C. columnatus* has brightly colored and very conspicuous basidiomata, the species has not been documented in the Galapagos during previous biological surveys (Jaramillo and Tye 2003; Jaramillo and Bungartz 2007; Bungartz et al. 2016).

Methods

We first observed basidiomata of *Clathrus columnatus* in 2020–2021 (not collected), but in July 2022 we collected three groups of specimens (four mature and eight immature fruiting bodies). All observations were made at 205 m a.s.l. in an agro-ecological farm on Santa Cruz Island (00°41′49″S, 090°20′54″W), Galapagos Islands, Ecuador (Fig. 1). All observations were in the lowland–highland transition zone of the island, where the mean annual rainfall is 4.4 mm (range: 0–115 mm) and the mean annual temperature is 20.8 °C (range: 16.2–25.2 °C). The farm where the specimens were found has an area of 6 ha and primarily grows vegetables, citrus, and banana. The farm was surrounded by native and endemic vegetation, dominated by *Scalesia pedunculata* Hook. f., *Darwiniothamnus tenuifolius* (Hook. f.) Harling, and *Pleuropetalum darwinii* Hook. f. Voucher specimens of *C. columnatus* were deposited at the Charles Darwin Research Station Herbarium, Galapagos (CDS); the herbarium code follows Thiers

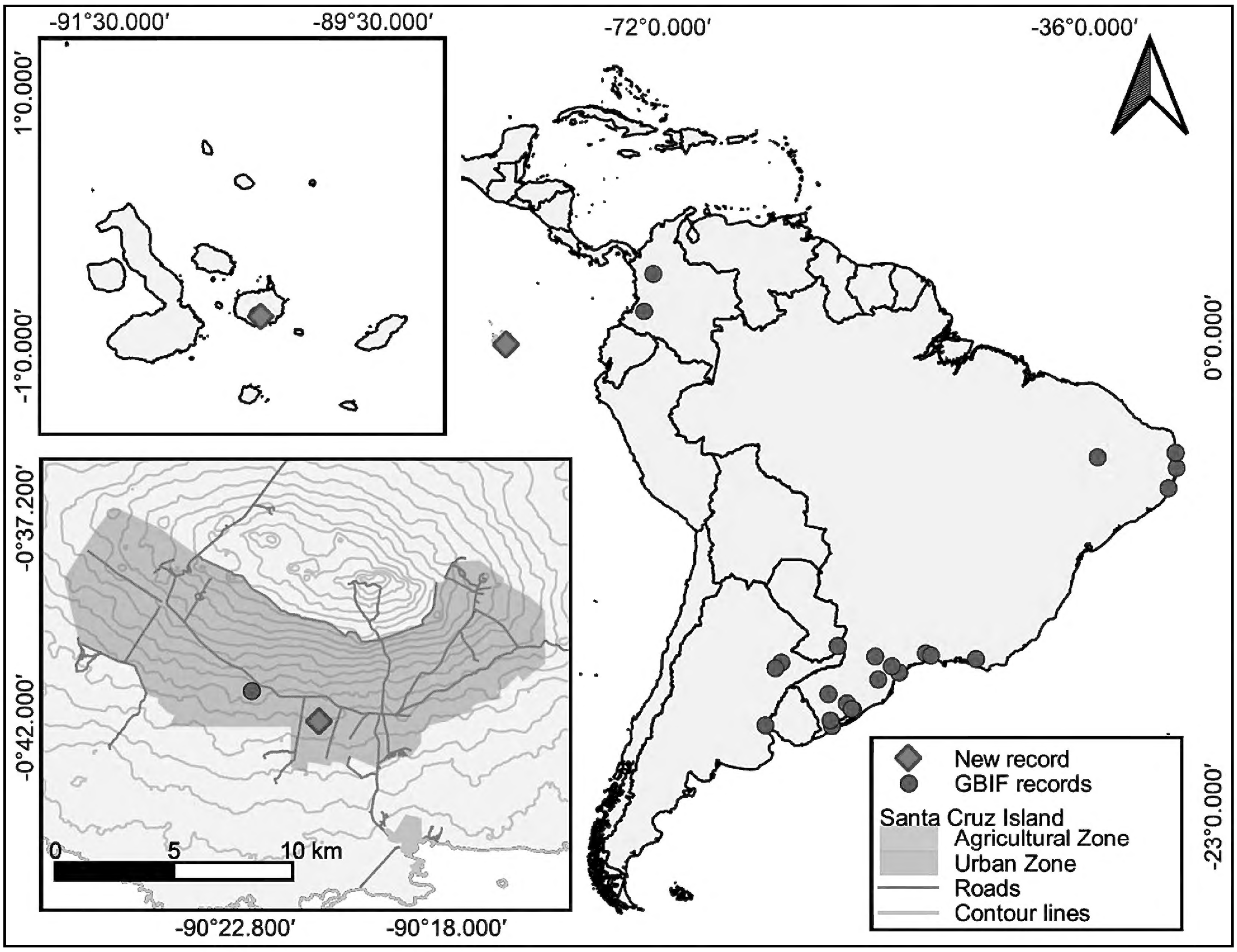

Figure 1. Distribution map of *Clathrus columnatus* in South America (georeferenced records from GBIF.org 2023).

(2023). Some basidiomata were dried in the herbarium plant drier for 6–10 h at 50–60 °C using incandescent light bulbs, while others were preserved in 70% ethanol.

In addition to our primarily specimen collection, we searched for records of Clathraceae on iNaturalist.

Description of macroscopic features of the basidiomata was based on fresh material and fluid-preserved specimens. For the microscopic analysis, portions of basidiomata were mounted and examined with a Carl Zeiss inverted microscope with an integrated Axiocam 705 color camera at 40× and 63× magnification. Anatomical structures were dyed with cotton-blue according to López and García (2019). Basidiospores and hyphae were measured using Zenlite and Image J software (Schneider et al. 2012). The spore quotient Qm was calculated representing the ratio of spore length vs spore width; the range of measurements, and their average (x ± SD, n = 25) are included (Largent et al. 1977). Identifications are based on descriptions by Dring (1980), Miller and Miller (1988), and Sandoval-Leiva et al. (2014).

Results

Clathrus columnatus **Bosc**, Mag. Gesell. naturf. Freunde, Berlin 5: 85 (1811)

Figures 2–4

New records. ECUADOR – **Galapagos** • Santa Cruz Island, Los Guayabillos, Darwin Ecogarden Farm; 00°41′49″S, 090°20′54″W; 200 m alt.; 6.VII.2022; J. Villalba-Alemán et al. 114 leg.; 7 dry basidiomata, CDS 58971 • ibid.; 28.VII.2022; J. Villalba-Alemán et al. 121 leg; 3 basidiomata in ethanol, CDS 58974 • ibid.; J. Villalba-Alemán et al. 123 leg; 1 dry basidiomata, CDS 58976A; 1 basidiomata in ethanol, CDS 58976B.

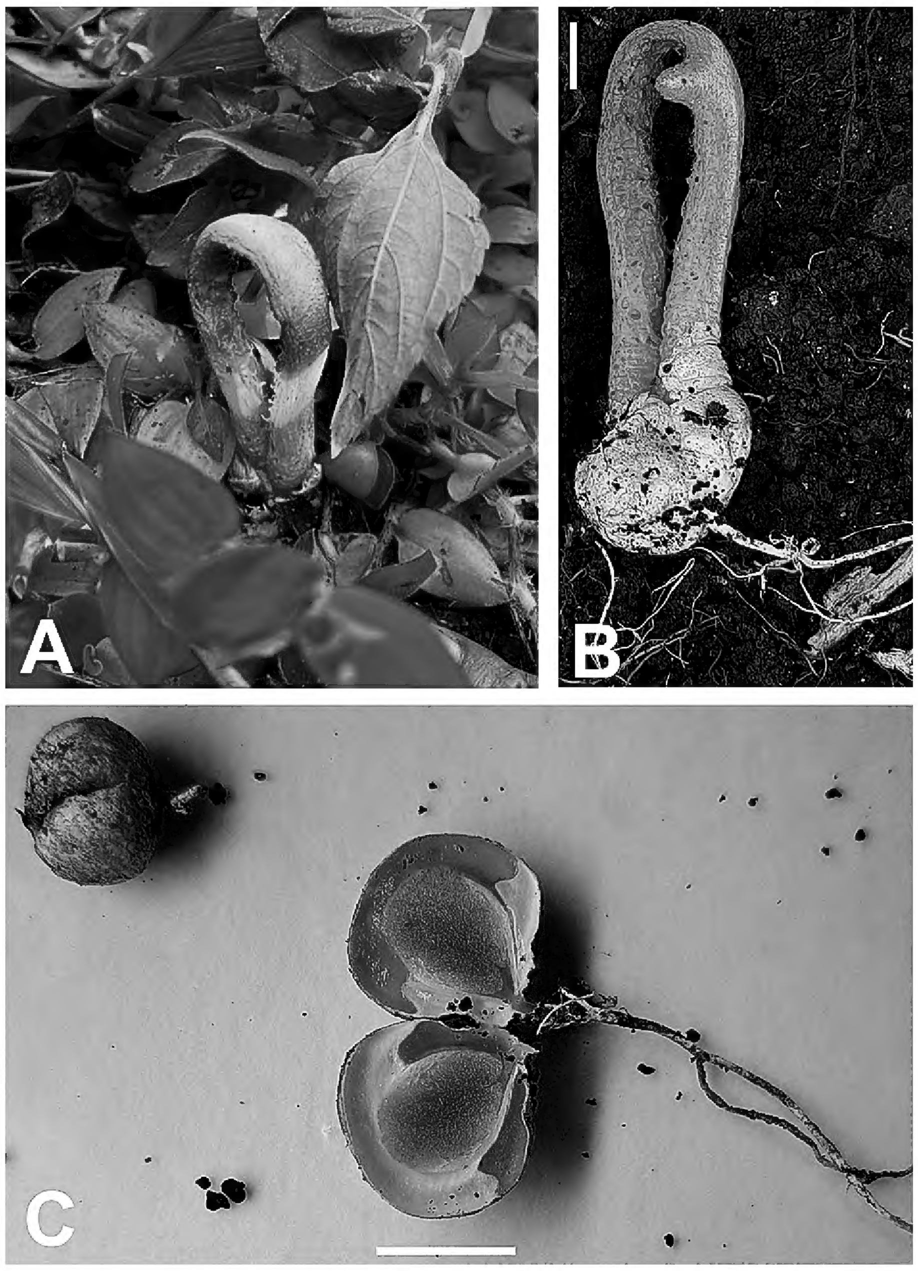

Figure 2. *Clathrus columnatus* CDS 58971. **A.** Basidioma in its habitat. **B.** Mature stage with volva and rhizomorphs exposed. **C.** Immature stage, one basidioma in longitudinal section. Scale bars: 1 cm.

Identification. Immature basidiomata epigeous, some of them semi-buried in the soil, globose to subglobose, "egg-shaped" with a slightly tuberculate texture, 0.3–2 × 0.4–2.5 cm, attached to long rhizomorphs forming a mycelial strand longer than 7 cm. Peridium was soft and moist when fresh, two-layered, with a creamy white exoperidium, ≤0.5 mm wide, and a transparent gelatinous endoperidium, 0.2–0.3 mm thick; in longitudinal section with a white to grayish gleba, 0.9 cm long × 0.7 cm wide; in transversal section forming 3 column vertices surrounded by the gelatinous layer, at the interior the gleba turning olivaceous green to brown. Mature basidiomata 3.0–9.8 cm tall, white volva (1.2–2.7 × 1.8–2.9 cm) very delicate and with some gelatinous mass inside. Receptacle with 2–4 "spongy" columns, free at base and fused at the apex, vibrant red in the apical zone but fading in color intensity to a soft red and orange at the base; columns 0.3–1.1 cm in diameter, porous, with residue of black gleba only at the internal superior part of the arch formed by the apically fused columns, no glebifers observed; multitubular columns with 7–10 chambers (in a transversal section) and apparently not connected; one specimen had a 1 cm protuberance below the apex in one of the columns (dimensions: 0.7 × 0.6 cm). Mycelial strand 0.15–0.22 cm wide at the base of the peridium.

Basidiospores 3.4–4.8 µm long × 1.2–2.1 µm wide (x = 4.2 ± 0.3 µm long × 1.8 ± 0.2 µm wide, n = 25) and Qm = 2.38; cylindrical, smooth surface, tinted blue in cotton-blue. Basidia observed in the parts of the glebal mass of dried material. Columns with pseudoparenchyma irregularly rounded cells, 18.8–31.9 µm in diameter. Exoperidium–volva turning blue when dyed with cotton-blue, external surface with septate, branched, partially inflated hyphae, 2.2–5.3(8.3) µm in diameter; internal gelatinous layer with septate, thin-walled (0.9–1.2 µm), hyphae, 2.8–8.1 µm in diameter, with clamp connections. Rhizomorph formed from bundles of filamentous hyphae, individual hyphae 1.1–1.3 µm in diameter.

iNaturalist observation. We found one report of *Clathrus* cf. *columnatus*, with research grade status, observed in 2020 on Santa Cruz Island (iNaturalistEc 2022). This observation was based on photographs of the basidiomata taken during a visit to see the agroforestry system of a farm (Velasteguí pers. comm. 2022). These specimens, although documented only by photos, have the same macroscopic characteristics as described for the species in the literature (e.g. columns fused at the apex, spore mass not confined to a glebifer), and they closely match the specimens we collected.

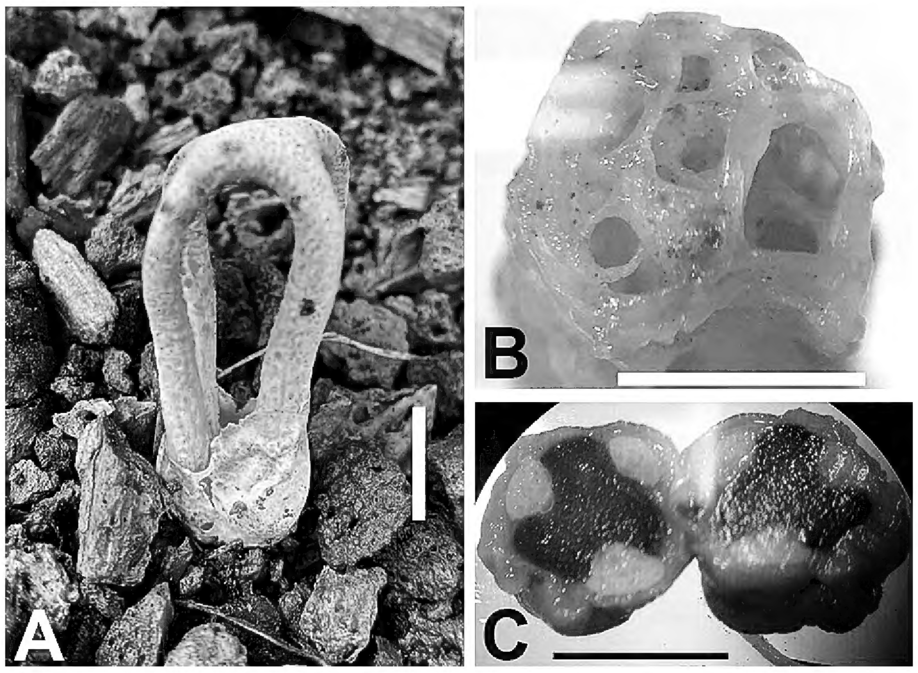

Figure 3. *Clathrus columnatus* CDS 58976. **A.** Fresh basidioma. **B.** Fluid-preserved 70% ethanol CDS 58974 column in transversal section. **C.** Immature basidioma in transversal section. Scale bars: A = 2 cm; B = 0.5 cm; C = 1 cm.

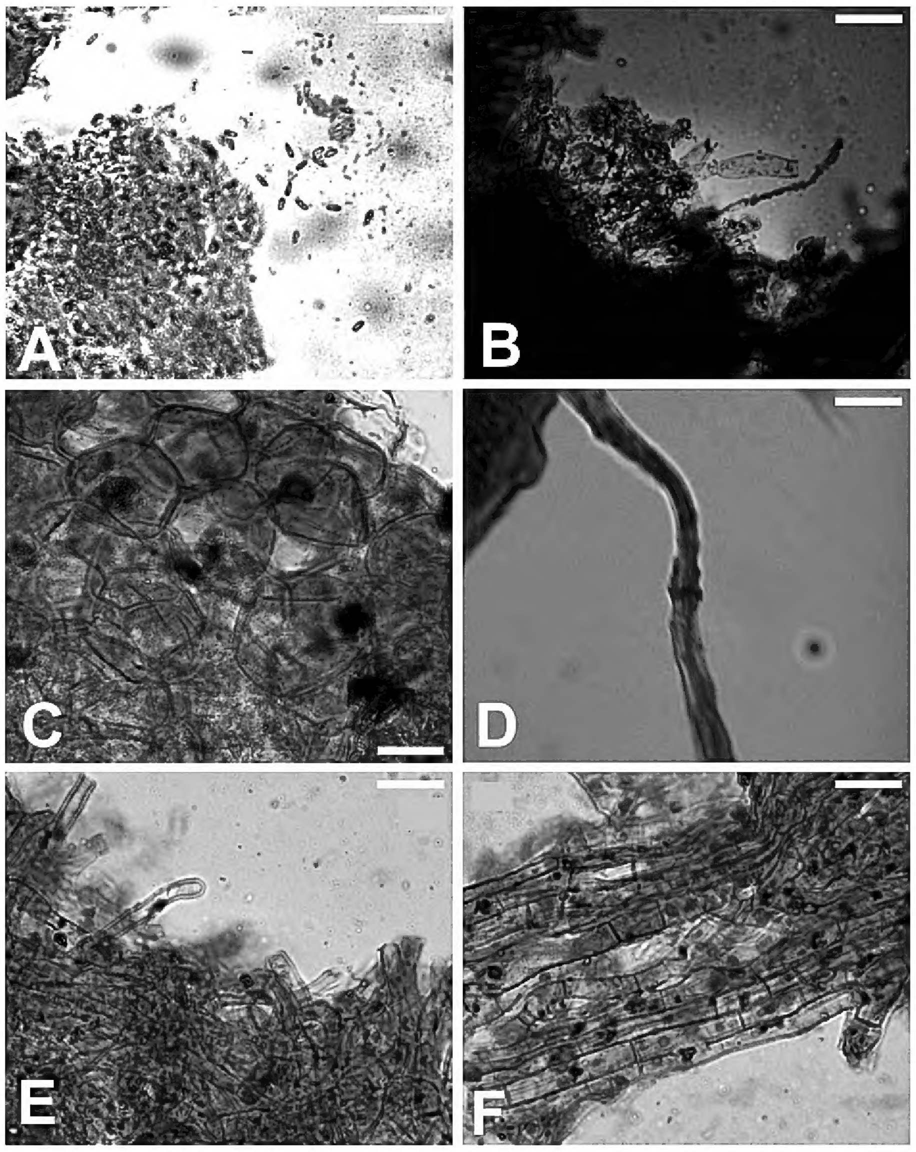

Figure 4. *Clathrus columnatus* microscopy. **A.** Spores. **B.** Basidia. **C.** Pseudoparenchyma. **D.** Septate hyphae of exoperidium. **E.** Thin-walled hyphae of endoperidium. **F.** Septate hyphae of gelatinous layer with clamp connections. Scale bars: 20 µm.

Figure 5. *Clathrus columnatus* habitat in the Galapagos Islands. **A.** *Musa* × *paradisiaca* roots. **B.** Immature basidioma with mycelial cord attached to *M.* × *paradisiaca* roots.

Habitat and ecology. Gregarious, on soil, growing in an open area with some planted bananas, *Musa* × *paradisiaca* L. Seven immature and one mature basidiomata (Group One) were observed during 5–6 of July 2022, within an area of approximately 0.25 m^2. These basidiomata were found among the herbaceous layer of the vegetation (10–15 cm high), predominantly composed of *Commelina diffusa* Burm. F. and *Oxalis debilis* Kunth. Immature basidiomata were partially or completely, but only superficially, buried within the soil, and the mycelial strands were attached to decomposing twigs. On 27–28 July 2022, we found two other groups (Groups Two and Three) of basidiomata approximately 10 m away from Group One. Group Two contained three old basidiomata and one basidiomata in the process of opening. All basidiomata in this group were epigeous, growing on a gravel trail, which had previously been covered by mulch, near the banana plantation. Basidiomata in Group Three were on the same trail, 5 m from Group Two, and included three overmature basidiomata and two small mature basidiomata. In Group Three, some immature basidiomata were found epigeous or superficially covered by soil; their large mycelial strands connected the basidiomata and attached also to the roots of *Musa* × *paradisiaca* (Fig. 5). These three records from July 2022 were approximately 3 km from the 2020 iNaturalist observation (Fig. 1).

Discussion

The basidiomata of *Clathrus columnatus* vary in shape and in the number of columns (2–5), are bright red to orange, have the columns fused at their apex but free at their base, and the glebal mass is spread along the internal portion of the columns (Magnago et al. 2013; Sandoval-Leiva et al. 2014; Campi Gaona et al. 2017; López and García 2019). Our specimens, which generally had four columns (consistent with Burt 1896), are macroscopically similar to *Laternea triscapa* Turpin, a species

sometimes confused with *C. columnatus* (Calonge et al. 2005). However, the latter species can be distinguished because the gleba is not confined to a glebifer. One of our specimens (CDS 58971) has a 1 cm protuberance below the apex, which could be a poorly developed column. Anomalies in the receptaculum have been noted elsewhere. For example, perforations in the apex are sometimes present in North American basidiomata (Chambers and Couch 1928; Dring 1980; López and García 2019). The spores in our specimens ranged between 3.0–5.0 μm long × 1.2–2.5 μm wide, which is generally consistent with specimens from United States, Mexico, Honduras, Brazil, East Africa, and New Zealand (Dring 1980; Magnago et al. 2013; López and García 2019). In contrast, Kotlaba and Zehnálek (2018) observed smaller spores (3–4 μm long) in Cuban material.

Like most Phallales, *Clathrus columnatus* is considered a saprotroph (Phillips et al. 2018; Põlme et al. 2020) and generally occurs in small groups in lawns and pastures (Trierveiler-Pereira et al. 2019) and on soil near woody debris in altered ecosystems (López et al. 1980; ColFungi 2023). It has been reported growing near *Pinus elliottii* Engelm. plantations in urban settings (Campi Gaona et al. 2017), but there is no clear indication that the two species are reliant on each other. In agricultural areas, *C. columnatus* was found in the early 1900s in sugar-cane fields in Hawaii, where it presumably was a parasite on the roots of *Saccharum officinarum* L. (Cobb 1906; Goos 1970; HEAR 2005). However, there is no recent evidence that *C. columnatus* is present in Hawaii (Hemmes and Desjardin 2009) or that it is a parasite anywhere else in the world. We are not aware of any other records of *C. columnatus* associated with banana plantations, which encourages further investigation into the association with this host.

Clathrus columnatus has been recorded in South America (Fig. 1), including Colombia (Vasco-Palacios and Franco-Molano 2012), Brazil (Magnago et al. 2013; Lima et al. 2019), Argentina (Domínguez 1985), Paraguay (Campi Gaona et al. 2017), and perhaps Chile (Sandoval-Leiva et al. 2014). Our records are the first confirmed from Ecuador. The observations of *C.* cf. *columnatus* that has been recently reported via iNaturalistEc (2023) in southern Ecuador should be examined prior to formally expanding the species' range. Novel records among distant localities reinforces the necessity for more fungal surveys throughout Ecuador, which include voucher specimens analyzed in detail (Filippova et al. 2022). Additional collecting efforts should be made for Phallales, which are hard to find in the field and are difficult to preserve (Magnago et al. 2013).

The basidiomata of *C. columnatus*, due to their ephemeral appearance and rapid consumption by insects (Trierveiler-Pereira et al. 2013), are difficult to observe and collect. Only 2–4 h elapse between the rupture of the peridium and the complete development of the receptaculum (Sáenz and Nassar 1982). As seen in the Galapagos, basidiomata usually remain intact for a couple hours to a few days (Guerrero pers. comm. 2022). Nonetheless, it seems very unlikely that such a conspicuous, brightly colored species would have been overlooked by all the investigators who have studied the vegetation and mycobiota in agricultural areas of Santa Cruz Island. Thus, it seems more likely that our records represent a relatively recent introduction of *C. columnatus.* It is plausible that this species was brought to the archipelago with agricultural products, as has been reported for many other introduced taxa now in the Galapagos (Toral-Granda et al. 2017). This hypothesis requires more investigation, and a molecular comparison of specimens from the Galapagos and mainland localities might elucidate the geographic source of *C. columnatus* on the archipelago. Molecular analyses have been used to trace the origins of other species introduced to Galapagos, such as the weevil *Galapaganus howdenae howdenae* Lanteri, 1992 (Sequeira et al. 2017) and guava *Psidium guajava* L. (Urquía et al. 2021).

Some *Clathrus* species are potential invaders of native ecosystems because of their high reproductive and dispersion capacities. The spread of *Clathrus* is likely promoted by entomochory (spore dispersal by insects; Tang et al. 2015). Also, as with most fungi, *Clathrus* can persist in their vegetative form and disperse by mycelial networks (Malloch and Blackwell 1992; Desprez-Loustau et al. 2007). For example, *Clathrus archeri* (Berk.) Dring, a species originally believed to be endemic to southern Africa, New Zealand, and Australia, is now successfully established in many regions of Europe and the Neotropics, with unknown consequences to the native mycobiota and decomposition dynamics (Desprez-Loustau et al. 2007; Pinzón-Osorio and Pinzón-Osorio 2020; Pietras et al. 2021). Further research remains necessary to better understand the distribution of *C. columnatus* and, thus, assess its ecological impact on the Galapagos Islands.

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Author Contributions

Conceptualization: JVA, PM, CMP, PJD. Data curation: JVA, PM. Formal analysis: JVA. Funding acquisition: PJD. Investigation: JVA. Methodology: JVA, PM, PJD. Resources: JVA, PM, CMP, PJD. Supervision: CMP, PJD. Visualization: JVA. Project administration: PJD. Writing – original draft: JVA, PM, PJD. Writing – review and editing: JVA, PM, CMP, PJD.

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